

EVALUATING MALLARD ADAPTIVE MANAGEMENT MODELS WITH TIME SERIES

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Abstract: Wildlife practitioners concerned with midcontinent mallard (*Anas platyrhynchos*) management in the United States have instituted a system of adaptive harvest management (AHM) as an objective format for setting harvest regulations. Under the AHM paradigm, predictions from a set of models that reflect key uncertainties about processes underlying population dynamics are used in coordination with optimization software to determine an optimal set of harvest decisions. Managers use comparisons of the predictive abilities of these models to gauge the relative truth of different hypotheses about density-dependent recruitment and survival, with better-predicting models giving more weight to the determination of harvest regulations. We tested the effectiveness of this strategy by examining convergence rates of “predictor” models when the true model for population dynamics was known a priori. We generated time series for cases when the a priori model was 1 of the predictor models as well as for several cases when the a priori model was not in the model set. We further examined the addition of different levels of uncertainty into the variance structure of predictor models, reflecting different levels of confidence about estimated parameters. We showed that in certain situations, the model-selection process favors a predictor model that incorporates the hypotheses of additive harvest mortality and weakly density-dependent recruitment, even when the model is not used to generate data. Higher levels of predictor model variance led to decreased rates of convergence to the model that generated the data, but model weight trajectories were in general more stable. We suggest that predictive models should incorporate all sources of uncertainty about estimated parameters, that the variance structure should be similar for all predictor models, and that models with different functional forms for population dynamics should be considered for inclusion in predictor model sets. All of these suggestions should help lower the probability of erroneous learning in mallard AHM and adaptive management in general.

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As articulated by Walters (1986), adaptive management provides a framework through which various forms of uncertainty about wildlife and fisheries populations are explicitly incorporated into the formulation of management decisions. In 1995, the U.S. Fish and Wildlife Service embraced adaptive management as an objective method for regulating the harvest of midcontinental mallards (U.S. Fish and Wildlife Service 2001). Federal and state waterfowl biologists perceived adaptive management as an impartial tool for pursuing the goal of maximizing cumulative harvest over time (Nichols 2000).

Under this adaptive management paradigm, researchers gain insight into the dynamics of mallard populations by comparing the predictive abilities of candidate models that express different hypotheses about population dynamics (Johnson et al. 1993, 1997, 2002; Nichols et al.

1995; Williams et al. 1996). Johnson et al. (1997) outlined 4 such predictor models used to express combinations of different hypotheses regarding survival (compensatory vs. additive mortality) and reproduction (strongly vs. weakly density dependent) in mallards. In an attempt to integrate further uncertainty, modelers have emulated random environmental variation, partial harvest control, and imprecision of key population parameter estimates. All such uncertainty sources are included in model predictions, such that each predictor model generates a distribution of population sizes that could result from a given set of harvest regulations. The relative credibility of each model can then be updated every spring according to how well its predictions match observed population size, through use of an empirical probability distribution (U.S. Fish and Wildlife Service 2001). Relative credibilities, in the form of model weights, are used to determine an optimal harvest strategy using a backward iteration stochastic dynamic programming (SDP) algorithm (Lubow 1995, Johnson et al. 1997). Learning, as such, occurs as model weights for 1

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of the predictor models converge toward 1, implying that the hypotheses behind the given model have best explained population dynamics over time relative to the other models evaluated. Such a model then becomes the primary basis for determining annual harvest regulations.

If this formulation of adaptive management is to work well, at least 2 key requirements must be met. First, if 1 of the models in the predictor model set captures the dominant mechanisms of population dynamics (what we shall call a "true" model), then model weights should converge to that model over time. Williams et al. (1996) examined learning rates of 2 of the mallard predictor models under different sets of harvest regulations and different levels of monitoring and harvest variation but did not evaluate the convergence properties of the full model set. In theoretical work on general ecological time series, Jost and Arditi (2000) explored model identification of predator-prey processes when the data included observation and process errors. They found that up to 15% of the time series resulted in misidentification of the correct model. Similarly, Carpenter et al. (1994) examined predator-prey model discrimination in plankton time series when both predictor and response variables were subject to error. Even modest amounts of error caused problems with model identification. Thus, the convergence properties of the adaptive management model set needs to be investigated.

Second, if the true model is not in the predictor model set, then the optimal harvest strategy generated through application of the mallard adaptive management framework should be similar to the optimal strategy for the true model. The validity of this second requirement has recently come under criticism. Runge and Johnson (2002) showed that different functional forms used to express hypotheses of mortality and reproduction in mallards can lead to quite different optimal harvest strategies. This can occur even if the functional forms predict similar population values over the range of observed data. This problem also has been well documented in the field of fisheries stock assessment (Hilborn and Walters 1992) and warrants a simulation exercise to determine which predictor models are favored when certain true models are not in the model set.

From 1995 until 2001, certain components of the mallard modeling process were considered deterministic, and no uncertainty was incorporated for natural mortality, crippling loss, seasonal

sex ratios, or model-specific recruitment functions. While care is needed to avoid extraneous compounding of sampling error, increasing the amount of uncertainty in model components may more accurately reflect our current knowledge of the system.

We assessed the efficiency of model selection for existing mallard population models when the true data were simulated from an *a priori* model. Given the obvious importance of previously formulated models in this context, we first reviewed the essential model structure underlying the 4 competing predictor models initially used in mallard adaptive management (see Johnson et al. 1997 for further explanation). Next, we developed several *a priori* models that could be used to simulate population dynamics. Specifically, we considered the 4 cases in which the *a priori* model comes from the historical predictor model set, as well as 2 cases when it did not. For the latter, we used a logistic form of density dependence in post-hunting season mortality as an alternative formulation of the compensatory mortality hypothesis (Johnson et al. 1993, Runge and Johnson 2002), as well as a partial compensation model for mortality (Caughley 1985, Conroy and Krentz 1990). We used these *a priori* models, along with a decision rule for harvest based on simulated observations of the system, to generate time series of system states (Walters and Green 1997). Finally, we examined convergence rates among historical predictor models when each *a priori* model was used to generate the data. We assessed the importance of the variance structure of the historical predictor model set in achieving convergence by considering different levels of uncertainty about the system.

HISTORICAL MODELING PERSPECTIVE

System Dynamics

Population models for the midcontinent mallard largely have focused on the timing of annual surveys, which permit estimation of key population parameters (Nichols et al. 1995, Smith 1995, Williams and Johnson 1995). In constructing these models, researchers sought to economize on model components such that models contain just enough biological structure to make them useful to managers. Thus, modelers avoided extrapolating from sparse data or including processes expected to have little effect on system predictions. We followed the models and notation for system dynamics presented by Johnson et

al. (1997) because as this formulation provided the basis for adaptively managing mallards from 1995 to 2001. System transitions are given by

$$X_{t+1} = X_t + F_i(X_t, H_t, z_t),$$

where X_t represents system state at time t , H_t denotes time-dependent harvests, z_t represents stochastic environmental effects between time t and $t+1$, and F_i specifies 1 of the models used to approximate population and habitat dynamics. In the particular case of midcontinent mallards, system state can be reduced to $X1_p$, or spring population size of mallards in the midcontinent survey area in year t , and $X2_p$, the number of ponds in Prairie Canada in spring of year t . "Prairie Canada" is defined as strata 26–40 (J. A. Dubovsky, U.S. Fish and Wildlife Service, personal communication) of the Breeding Waterfowl and Habitat Survey (U.S. Fish and Wildlife Service 2000) and comprises portions of southern Alberta, Saskatchewan, and Manitoba.

Changes in population size traditionally have been modeled as a function of mortality and reproduction only. While a small amount of immigration and emigration occurs, these are limited because migration occurs largely within flyways and individuals must change migration patterns to move into or out of a different population. The effects of immigration and emigration in midcontinent mallards have been ignored by modelers because the increased complexity resulting from including these variables contributes little to accurate predictions about system state (J. D. Nichols, U.S. Geological Survey [USGS], personal communication). Thus, model-specific transitions in population size have been written as

$$X1_{t+1,s} = X1_{t,s}\phi_{i,t,s} + y_{i,t,s}\phi'_{i,t,s},$$

where $\phi_{i,t,s}$ and $\phi'_{i,t,s}$ represent model, time, and sex-dependent survival probabilities for adult and juvenile mallards, respectively, and where

$$y_{i,t,s} = g_i(X1_{t,s}, X2_t),$$

is a model-dependent recruitment function. We defined "recruitment" as the number of juvenile mallards surviving until the fall harvest, even though these individuals are assumed to function as juveniles until they reach their first breeding season. This definition is necessary because the first information about juveniles comes from adjusted age ratios of wings submitted by hunters

(Cowardin and Blohm 1992). Note also that this formulation of recruitment depends on both adult population size and number of ponds. The number of ponds in Prairie Canada is an important component in determining the overall quality of mallard breeding grounds (Pospahala et al. 1974, Johnson et al. 1992).

The Johnson et al. (1997) Model Set

Johnson et al. (1997) identified 4 models for mallard population dynamics that reflect structural uncertainty about the processes of reproduction and mortality. We let models $S_C R_S$, $S_A R_S$, $S_C R_W$, and $S_A R_W$ designate combinations of the completely compensatory (S_C) and completely additive (S_A) mortality hypotheses with the weakly density-dependent (R_W) and strongly density-dependent (R_S) recruitment hypotheses (U.S. Fish and Wildlife Service 2001). These 4 models and their relative predictive abilities, constituted the basis for mallard adaptive management from 1995 to 2001.

Mortality Hypotheses.—Despite decades of historical data from 1 of the best continental monitoring systems in the world, considerable disagreement remains about the appropriate model to use for harvest mortality (Nichols 1991, Smith and Reynolds 1992, Johnson et al. 1993, Nichols et al. 1995). Absence of true statistical replication, lack of random assignment of harvest regulations to different population sizes, and a variety of other sources of uncertainty combine to limit our ability to distinguish important relationships (Nichols 1991, Nichols et al. 1995). Political pressures also have limited the ability of wildlife managers to learn about population dynamics through experimentation with harvest regulations (Nichols 2000). In practice, 2 extreme hypotheses have been used to express uncertainty about the correct form of harvest mortality. The additive hypothesis (S_A) posits that annual survival rates are strictly proportional to mortality incurred during the hunting season. The compensatory hypothesis (S_C), on the other hand, predicts that annual survival rates will be unaffected when harvest rates are below a certain threshold (Anderson and Burnham 1976). Historical tests for evidence of density dependence in mallard survival have focused largely on these models (e.g., Anderson and Burnham 1976, Nichols et al. 1984, Smith and Reynolds 1992). This dichotomy is somewhat artificial; the best-approximating model for density-dependent survival is certainly somewhere in between these extremes (Guthery 2002).

Partly because of historical tradition and partly because of uncertainty about the exact mechanism for compensatory mortality, the functional forms for additive and compensatory mortality have been formalized in phenomenological models (Williams et al. 1996, Johnson et al. 1997). Annual survival is broken down into seasonal components,

$$\phi_{i,t,s} = \alpha_s \beta_{i,t,s} \gamma \text{ and } \phi'_{i,t,s} = \beta'_{i,t,s} \gamma,$$

where α_s is sex-specific adult summer survival, $\beta_{i,t,s}$ and $\beta'_{i,t,s}$ are hunting season survival for adults and young, respectively, and γ is winter survival. The component for hunting season survival is manipulated to express the compensatory and additive hypotheses (Fig. 1). For the additive mortality hypothesis, hunting season survival is given by

$$\beta_{i,t,s} = 1 - \frac{h_{t,s}}{1-h} \text{ for adults,}$$

$$\text{and } \beta'_{i,t,s} = 1 - \frac{h'_{t,s}}{1-c} \text{ for juveniles,}$$

where $h_{t,s}$ and $h'_{t,s}$ are time- and sex-dependent harvest rates for adult and juvenile mallards, and c is crippling loss. For the compensatory hypothesis, hunting season survival is given by

$$\beta_{i,t,s} = \begin{cases} 1.0, & \text{if } \frac{h_{t,s}}{1-c} \leq 1 - \alpha_s \gamma \\ \frac{1 - \frac{h_{t,s}}{1-c}}{\alpha_s \gamma}, & \text{if } \frac{h_{t,s}}{1-c} > 1 - \alpha_s \gamma \end{cases} \quad \text{for adults, and}$$

$$\beta'_{i,t,s} = \begin{cases} 1.0, & \text{if } \frac{h'_{t,s}}{1-c} \leq 1 - \alpha_s \gamma \\ \frac{1 - \frac{h'_{t,s}}{1-c}}{\alpha_s \gamma}, & \text{if } \frac{h'_{t,s}}{1-c} > 1 - \alpha_s \gamma \end{cases} \quad \text{for juveniles.}$$

Note that in this completely compensatory phenomenological model, no mortality is assumed for the hunting season unless the number of mallards harvested exceeds the number that will die due to natural causes during the rest of the year (often up to 15% of the population).

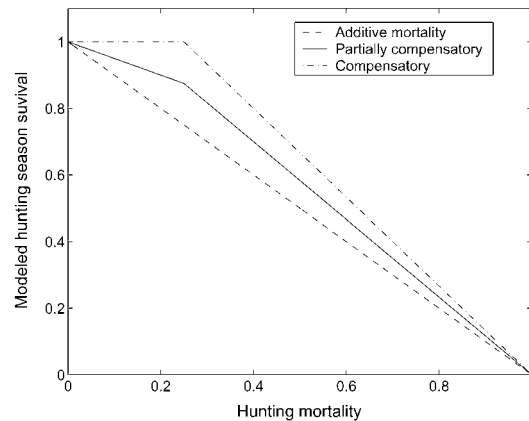


Fig. 1. Graphical representation of historically formulated compensatory, additive, and partially compensatory mortality hypotheses (Conroy and Krementz 1990, Williams et al. 1996) for midcontinent mallards. For the additive model, harvest mortality is strictly proportional to harvest rate, while the compensatory model posits that harvest mortality is zero unless harvest rate surpasses some threshold value. The partially compensatory hypothesis we used was halfway between the additive and compensatory models.

Reproductive Hypotheses.—Johnson et al. (1997) identified 2 models to represent hypotheses of strongly density-dependent and weakly density-dependent reproduction. They used Akaike's Information Criterion (AIC; Akaike 1974, Burnham and Anderson 1998) to identify an appropriate model for recruitment and parameterized the model differently (using a confidence ellipsoid approach) to express the 2 recruitment hypotheses. Population size and number of prairie ponds in the spring were identified as important determinants of fall recruitment. The 2 models for recruitment, entering into the balance equations in the form of fall age ratios, are given by

$$R_{W,t} = 0.8249 - 0.0547 \times 10^{-6} X1_t + 0.1130 \times 10^{-6} X2_t$$

for weakly density-dependent recruitment, and

$$R_{S,t} = 1.1081 - 0.1128 \times 10^{-6} X1_t + 0.1460 \times 10^{-6} X2_t$$

for strongly density-dependent recruitment, where W and S represent weak and strong density dependence, respectively, and t denotes time dependency.

Partial Harvest Control.—To address uncertainty regarding the relationship between harvest regulations and harvest rate, Johnson et al. (1997) fit gamma distributions to adult male harvest rates that were associated with particular periods of

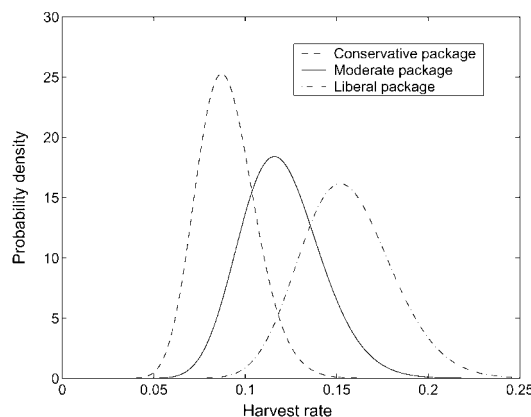


Fig. 2. Distributions of harvest rates associated with conservative, moderate, and liberal packages of harvest regulations (Johnson et al. 1997) for midcontinent mallards.

restrictive, moderate, and liberal harvest regulations (Fig. 2). These harvest packages correspond to mean harvest rates of 0.09, 0.12, and 0.156, respectively. Differential vulnerabilities to harvest were calculated for juvenile males, juvenile females, and adult females in relation to adult males to determine their respective harvest rates.

Environmental Variation.—Johnson et al. (1997) showed that the annual change in the number of ponds in Prairie Canada could be modeled as

$$X2_{t+1} = -3,835,087.53 + 0.45X2_t + 13,695.47r_t,$$

where r_t follows a normal distribution with mean 418 and variance 3,136. While some of the mathematical features of this model are unrealistic (e.g., not restricting the number of ponds to be positive), the model has been shown to work well over the range of observed data (Johnson et al. 1997).

Partial Observability.—Estimation of key population parameters usually involves substantial sampling error. We included observation error in determining population size and number of ponds in Prairie Canada each spring in the modeling process, as well as stochastic change in partial vulnerabilities to harvest. These errors have been assumed to follow normal distributions (U.S. Fish and Wildlife Service 2001).

Updating Model Weights.—Johnson et al. (1997) suggested a method whereby regulatory decisions would be based on the relative predictive abilities of the 4 candidate population models, which can be measured in the form of model weights. This method follows the general approach described by Walters (1986). The predictive abilities of the

4 models were updated each year depending on how well they performed in forecasting population size. The mechanism for updating model weights is based on Bayes' theorem:

$$l_{i,t+1} = \frac{l_{i,t}p_i(X1_t, X1_{t+1})}{\sum_i l_{i,t}p_i(X1_t, X1_{t+1})},$$

where the updated model weight ($l_{i,t+1}$) depends on the prior model weight ($l_{i,t}$) and the model specific probability of observing the realized population size at time $t+1$ ($p_i(X1_t, X1_{t+1})$).

Dynamic Optimization.—Given a set of model weights characterizing knowledge of the system, Johnson et al. (1997) used SDP (Lubow 1995) to find state-dependent optimal harvest strategies. Optimal solutions were obtained in accordance with an objective function, which formalized the goals of mallard management. While the exact form of the objective function is beyond the scope of this paper, it represents a compromise between the dual goals of maximizing cumulative harvest over an extended time frame and keeping midcontinent mallard population size above 8.1 million birds in the traditional breeding survey area, a target established by the North American Waterfowl Management Plan (U.S. Department of the Interior and Environment Canada 1986).

METHODS

Predictor Model Sets

We considered 3 sets of predictor models assuming different levels of uncertainty about the system. We used the Johnson et al. (1997) model set and considered sources of variation corresponding to:

Level 1—the original model set,

Level 2—the original model set, but including additional variance associated with recruitment predictions, and

Level 3—those described in Level 2, as well as variance components associated with nonhunting season survival.

To introduce variation into the 2 recruitment functions, we first computed a mean squared error for each recruitment model (MSE_i) by fitting the models to observed data on recruitment, population size, and number of Prairie Canada ponds from 1970 to 1993. We then used estimates of spring population size ($\hat{X1}_t$) and number of spring ponds in Prairie Canada ($\hat{X2}_t$) to compute

an $(X'X)^{-1}$ matrix. The variation of a single prediction for each model was then computed as

$$\hat{V}(\text{predicted } R_{i,t}) = [1 + X_0(X'X)^{-1}X_0'] \times MSE_p$$

where $X_0 = [1 \ \hat{X}1_t \ \hat{X}2_t]$ (Steel et al. 1997) and

$$X = \begin{bmatrix} 1 & \hat{X}1_{1970} & \hat{X}2_{1970} \\ 1 & \hat{X}1_{1971} & \hat{X}2_{1971} \\ \vdots & \vdots & \vdots \\ 1 & \hat{X}1_{1993} & \hat{X}2_{1993} \end{bmatrix}.$$

For Level 3 uncertainty, we further introduced variability by assigning a coefficient of variation (CV) of 0.10 to nonhunting season survival sources.

Establishing A Priori Models

We first considered versions of the 4 models established by Johnson et al. (1997) as possible a priori models for population dynamics of mallards. We assumed that the true population size was determined stochastically according to the Level 1 uncertainty structure but with a slight modification to include stochastic variation in recruitment at a given level of mallards and ponds (i.e., process error). We used the models

$$R_{S,t} = 1.1081 - 0.1128 \times 10^{-6} X1_t + 0.1460 \times 10^{-6} X2_t + v_{S,t}$$

for strong density dependence, and

$$R_{W,t} = 0.8249 - 0.0547 \times 10^{-6} X1_t + 0.1130 \times 10^{-6} X2_t + v_{W,t}$$

for weak density dependence, where $v_{S,t}$ and $v_{W,t}$ represented process error for strongly and weakly density-dependent recruitment, respectively. Values for $v_{S,t}$ and $v_{W,t}$ were determined at each time step by simulating random normal variates with mean zero and variances 0.0082 and 0.0059, respectively (see Appendix A for derivation of variances). While some restrictive assumptions were needed to obtain distributions for recruitment process error, we maintain that the importance of considering cases where the a priori model has both more and less variability than the predictor model set justified our approach.

We next considered cases where the a priori model used to generate population dynamics was not in the predictor model set. We considered a logistic model for density-dependent mortality following the hunting season as an alternative articu-

lation of the compensatory hypothesis (Johnson et al. 1993, Runge and Johnson 2002), as well as a partial compensation model for mortality (Caughley 1985, Conroy and Krementz 1990). While parameterizing these models with field data has been difficult in practice (Conroy and Krementz 1990, Runge and Johnson 2002), we agree with Runge and Johnson (2002) that specifying the correct functional form for population dynamics often may be more important than precise parameter estimation. In this context, we note that partial compensation models do not specify a mechanism for density dependence. Consequently, they fall victim to the same flaws as the fully compensatory model when determining an optimal harvest strategy (Runge and Johnson 2002). Using a partial compensation model, however, is illustrative in that it represents the combination of hypotheses used in the current mallard adaptive management paradigm.

Partial compensation hypotheses are not well defined because any model intermediate between the compensatory hypothesis and the additive hypothesis could be termed partially compensatory (Conroy and Krementz 1990). Thus, the choice of compensatory threshold and slope parameters is arbitrary. From a management standpoint, however, the value of selecting between alternative models is greatest when their optimal harvest strategies dictate different management actions (Walters 1986, Johnson et al. 1993, Williams et al. 1996). Therefore, we chose parameters that placed the partially compensatory model for mortality equidistant from both the additive and compensatory models (Fig. 1). Hunting season mortality was thus modeled as:

$$\beta_{i,j,s} = \begin{cases} 1 - \frac{h_{i,s}}{2(1-c)}, & \text{if } \frac{h_{i,s}}{1-c} \leq 1 - \alpha_s \gamma \\ \frac{-(1 + \alpha_s \gamma)}{2\alpha_s \gamma} \times \left(\frac{h_{i,s}}{1-c} - 1 \right), & \text{if } \frac{h_{i,s}}{1-c} > 1 - \alpha_s \gamma \end{cases}$$

for adults, and

$$\beta'_{i,j,s} = \begin{cases} 1 - \frac{h'_{i,s}}{2(1-c)}, & \text{if } \frac{h'_{i,s}}{1-c} \leq 1 - \alpha_s \gamma \\ \frac{-(1 + \alpha_s \gamma)}{2\alpha_s \gamma} \times \left(\frac{h'_{i,s}}{1-c} - 1 \right), & \text{if } \frac{h'_{i,s}}{1-c} > 1 - \alpha_s \gamma \end{cases}$$

for juveniles.

Apart from the difference in mortality components, true population sizes were generated the same way as when the a priori model was 1 of the models in the model set.

Density dependence is often cited as the dominant mechanism for compensatory relationships in wild populations (Johnson et al. 1993, Boyce et al. 1999, Runge and Johnson 2002). Factors such as migration distance, food availability, quality of habitat, and predation rate may be affected by population density (Johnson et al. 1992), and hence may contribute to density-dependent changes in mortality following the hunting season. We next considered a seasonally explicit model for density dependence (Boyce et al. 1999) in the form of a logistic winter survival model (Runge and Johnson 2002). In this model, winter survival rates were assumed to be inversely proportional to post-harvest population size. Time- and sex-specific winter survival is given by

$$\lambda_{st} = F[P_t] = \left[s_{0s} + (s_{1s} - s_{0s}) \left(\frac{1 + e^{-m c_s}}{1 + e^{m(P_t - c_s)}} \right) \right] \times \frac{1}{\alpha_s},$$

with the constraints

$$m > \frac{1}{K} \ln \left(\frac{2(s_{1s} - \phi_s)}{\phi_s - s_{0s}} + 1 \right), \text{ and}$$

$$c_s = \frac{1}{m} \ln \left(\frac{\phi_s - s_{0s}}{s_{1s} - \phi_s} (e^{mK} - 1) - 1 \right),$$

where α_s is sex-specific summer survival, P_t is post-harvest population size assuming the additive model for hunting season survival, s_{0s} and s_{1s} specify sex-specific minimum and maximum survival rates outside the hunting season, ϕ_s is sex-specific total annual survival rate in the absence of harvest, and K determines the inflection point. The shape parameter (m) determines the degree of concavity in the relationship between post-harvest population size and winter survival.

Mechanistic models for density dependence, such as this one, have been difficult to parameterize in practice because of the lack of data. Nevertheless, we explored whether such models could better represent reality than phenomenological models. Other mechanistic models could have been considered in this context; for instance, density-dependent models in which winter survival was a function of wintering ground density (post-harvest population size divided by a measure of suitable winter

habitat) or amount of available habitat (Guthery 1997) would have been viable alternatives. However, no field data on wintering ground habitat conditions (e.g., number of ponds) were available.

Because of difficulties involved with parameterizing the logistic model from data, we added and subtracted a CV of 0.2 from mean estimated survival outside of the hunting season to specify s_0 and s_1 for female and male mallards. We made additional constraints for s_1 so that winter survival could not take on values >1.0 . The mean estimates of survival were used to specify values for ϕ_s . We assumed summer survival was constant over time for both sexes because large-scale monitoring data had failed to produce firm evidence that density dependence occurs during the summer at the midcontinental scale (W. L. Kendall, USGS, and D. I. MacKenzie, Proteus Research and Consulting, unpublished data). Reasonable values for m and k were chosen so that changes in winter survival due to high density would produce noticeable effects after post-harvest population size exceeded 8 million individuals. Resulting logistic equations differed only slightly for males and females, so we used the intermediate model

$$\lambda_t = .72 + .28 \times \left(\frac{1 + e^{-6}}{1 + e^{\frac{P_t}{2000000} - 6}} \right)$$

to represent density-dependent winter survival for both sexes (Fig. 3).

Structure of Simulation

Generating True and Observed System States.— Given an a priori model for population dynamics,

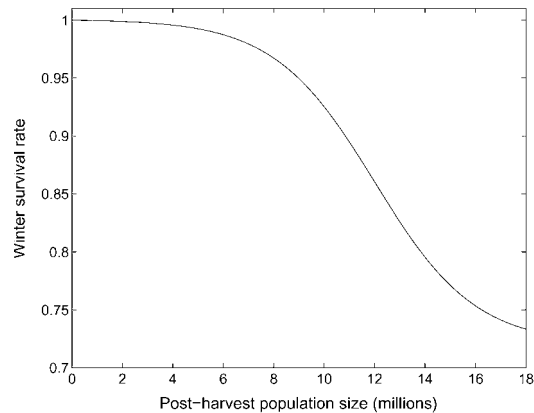


Fig. 3. Logistic model for seasonal winter survival of midcontinent mallards following the harvest season as an alternate form of the compensatory hypothesis.

we generated a realized population size for the spring of year $t + 1$ that depended on population size, number of prairie ponds, and harvest decision in year t (Fig. 4). The annual number of prairie ponds was simulated according to the Markovian model (Johnson et al. 1997) but was constrained to be >1 million to prevent negative values. We then added simulated sampling error to the simulated true population size and number of ponds to generate observed system states, thus emulating annual spring surveys.

Automating Harvest Decisions.—In an effort to mimic the process of adaptive management as described in Johnson et al. (1997), we set simulated harvest regulations according to a weighted average of predictor model weights. In the real world, harvest decisions from 1995 to 2001 were made using SDP (Lubow 1995), but interfacing SDP with MATLAB, the programming language we used for simulation, presented difficulties. To address this problem, we utilized the harvest matrices presented in Johnson et al. (1997), which specified optimal harvest packages for each of the models $S_C R_S$, $S_A R_S$, $S_C R_W$, and $S_A R_W$ given a particular value of observed ponds and population size. We assigned indicators of zero, 1, 2, and 3 to the harvest regulation packages corresponding to closed season, conservative, moderate, and liberal, respectively. We then obtained annual harvest packages by using the most recent model weights and associated optimal packages in a weighted average, rounding to the nearest integer, and using the package associated with

that integer. In general, the resulting simulated harvest decision was given by

$$D = \text{round} \left(\frac{l_{CS} d_{CS}^* + l_{AS} d_{AS}^* + l_{CW} d_{CW}^* + l_{AW} d_{AW}^*}{4} \right),$$

where l is model weight and d is the optimal harvest decision for each individual model. Possible harvest strategies were $d = 0$ (closed season), $d = 1$ (conservative harvest), $d = 2$ (moderate harvest), and $d = 3$ (liberal harvest). In this manner, model weights supporting the compensatory mortality hypothesis will lead to more liberal harvest decisions than model weights supporting the additive mortality hypothesis.

Generating Predictions.—We used parametric bootstrapping to generate model-specific empirical distributions of predicted population size observations (U.S. Fish and Wildlife Service 2000). We assumed normal distributions for each uncertainty component (with the exception of harvest rates, which we assumed to follow a gamma distribution). For each iteration, random variates from each of the uncertainty components were combined in the modeling process to produce a single predicted population size. For each model, we used 10,000 such iterations to approximate a random sample from the predicted population size distribution. We then used kernel density estimation to approximate the underlying probability density, using normal kernels and assuming an optimal bandwidth based on results from the normal distribution

(Silverman 1986, Simonoff 1996). Non-parametric choices for bandwidth are possible (see Silverman 1986, Simonoff 1996, Hazelton 1999), but the requisite computing time was irreconcilable with the sheer quantity of simulations required. Underlying probability densities for predictive distributions were unimodal and resembled normal distributions, so we did not expect this to be a large source of error. The relative probability ($p_i(X1_t, X1_{t+1})$) of observing population size $X1_{t+1}$ at time

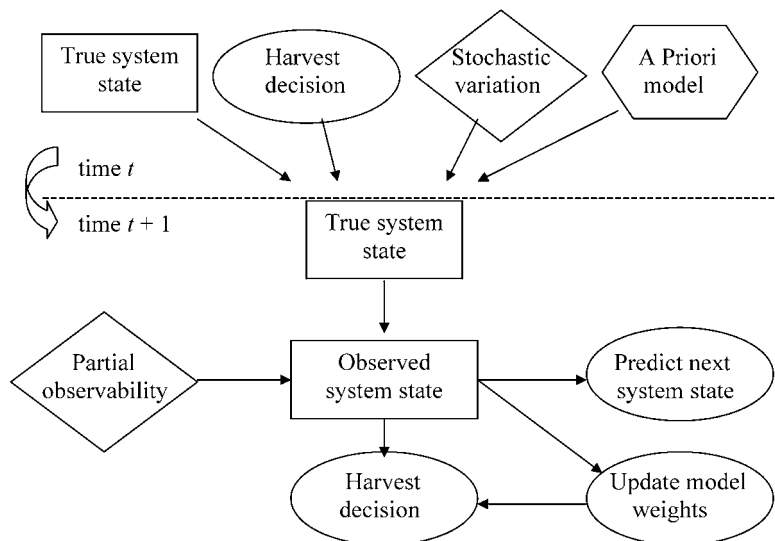


Fig. 4. Simulation structure describing the relationship between midcontinent mallard harvest decisions, model predictions, and true and observed population sizes.

$t+1$, given that model i is true, could then be obtained by evaluating the observed population size ($X_{1,t+1}$) on the smoothed distribution for model i . Using these probability densities, model weights were updated on a yearly basis. A uniform distribution of predictor model weights was assumed at the start of all simulations.

Number of Simulations.—Given an a priori model, we used 4, 7, 10, and 13 million mallards as initial values for population size and 1.5, 3.75, and 6 million ponds as initial values for number of prairie ponds. When the a priori model was in the model set, combinations of initial values, in addition to the 3 levels of assumed certainty and 4 possible a priori models, led to a total of 144 independent simulations. For the case when the a priori model was not in the model set, we limited the number of uncertainty sources to Levels 1 and 2 to reduce computing time. Still, factoring in different initial values for spring ponds and population size, 2 possible recruitment models, and 2 levels of uncertainty led to an additional 96 simulations. For each simulation, we used 50 iterations of 50-year time series to provide replication in simulation. Total central processing unit time for all simulations was approximately 800 hr (34 days) on a 330 MHz Sun Ultrasparc 10 floating point processor.

Analysis of Simulation

Convergence of predictor model weights to a particular model was a somewhat elusive criterion to define. In examining learning rates of 2 adaptive management models, Williams et al. (1996) reported average model weights and associated standard deviations after 8 years of simulation time. Similarly, for cases in which the a priori model was not in the model set, we described average model weights and accompanying standard errors at landmarks of 3, 8, 15, 30, and 50 years of simulation time. For cases in which the a priori model is in the predictor model set, we reported average model weights as well as a measure of predictor model convergence. We defined convergence to occur in an individual iteration if the predictor model weight associated with the a priori model surpassed 0.95. Mean times to convergence were determined for collections of simulation replicates that displayed convergence within the 50-year time series. Once convergence occurred, we further reported the percentage of simulation time that a model's weight fell below the 0.95 threshold as a measure of the strength and stability of convergence.

RESULTS

Predictor Model Set

For the case when the a priori model was a variant of 1 of the 4 models in the model set, model $S_C R_W$ converged the fastest, followed by models $S_A R_S$ and $S_A R_W$ (Fig. 5, Table 1). However, on average, model $S_C R_S$ did not exhibit stability with regard to convergence. When model $S_C R_S$ was used to generate time series, individual replications were characterized by shared or switching model weight between models $S_C R_S$ and $S_A R_W$. On average, $S_C R_S$ predicted better, but the 2 models often predicted very similar population sizes over the range of observed data (Fig. 6). The added process error in the recruitment function of the a priori model resulted in occasional true population sizes outside the range of predicted population sizes for level 1 uncertainty predictor models (Fig. 7). When this happened, other predictor models rapidly gained model weight. This led to "switching" model weights (Fig. 8A). Under increased levels of uncertainty in the predictor model set, changes in model weights over short time periods were much less pronounced (Fig. 8B).

Partial Compensation

When the partially compensatory model for survival was combined with the strongly density-dependent recruitment model (model $S_P R_S$) to generate true population sizes, predictor model $S_A R_W$ frequently dominated harvest decisions, with model $S_A R_S$ contributing somewhat as well (Table 2). For both levels of predictor uncertainty, model weights increased on average to around 0.94 for model $S_A R_W$ and to approximately 0.06 for model $S_A R_S$. Standard errors for average model weights were greater under Level 1 uncertainty than under Level 2 uncertainty, indicating a propensity for greater fluctuations in model weight during individual replications. Neither compensatory predictor model ($S_C R_S$ or $S_C R_W$) contributed substantially to harvest decisions, with model weights tending toward zero over time.

When partial compensation was combined with weakly density-dependent recruitment (model $S_P R_W$), predictor model $S_A R_W$ continued to dominate many harvest decisions, although model $S_C R_W$ also garnered a substantial amount of model weight. Average model weights were similar for both levels of uncertainty (Table 2). Under Level 1 uncertainty, individual iterations were characterized by extended periods of high model weights for 1 of the 2 models, with rapid transitions in model weight

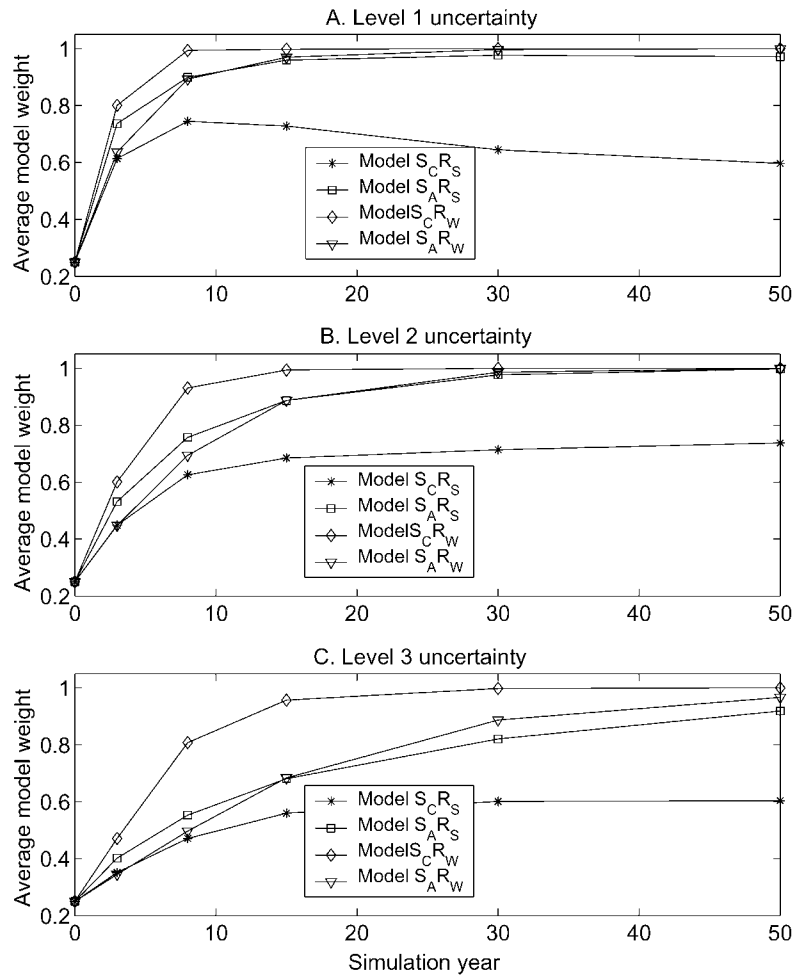


Fig. 5. Average model weights over 50 years of simulation time of midcontinent mallard abundance when the a priori model was in the model set. A priori models represent combinations of compensatory (S_C) or additive (S_A) mortality and strongly (R_S) or weakly (R_W) density-dependent recruitment. Model weights are given for the model used to generate the data under (A) Level 1 Uncertainty, (B) Level 2 Uncertainty, and (C) Level 3 Uncertainty.

following particularly bad predictions. This phenomenon is reflected in high standard errors for average model weights (Table 2). Under Level 2 uncertainty, neither model usually dominated harvest decisions. Rather, time series were characterized by shared model weight between predictor models $S_A R_W$ and $S_C R_W$. Under the 2 levels of uncertainty, neither of the models assuming strongly density-dependent recruitment ($S_C R_S$ and $S_A R_S$) contributed substantially to harvest decisions (i.e., model weight approaches zero over time).

Logistic Winter Survival

Combining logistic winter survival with strongly density-dependent recruitment (model $S_L R_S$) to generate true population sizes favored predictor

models incorporating additive survival ($S_A R_S$ and $S_A R_W$; Table 3). Replications under Level 1 uncertainty were characterized by convergence to 1 of the additive models. In general, model $S_A R_W$ converged more often, but model $S_A R_S$ did much better when initial values for population size and pond number were high. Under Level 2 uncertainty, time series were characterized by shared model weight between models $S_A R_S$ and $S_A R_W$, with neither model usually dominating. Model weight for the compensatory models approached zero under both levels of uncertainty.

When the logistic survival model was combined with weakly density-dependent recruitment, model $S_A R_W$ almost always dominated harvest decisions. Under both levels of uncertainty, the model weight for $S_A R_W$ approached 1 over time (Table 3). However, Level 1 uncertainty did lead to faster learning rates than Level 2 uncertainty. The

mean spring population size for mallards under all initial conditions and uncertainty sources was approximately 9.26 million under logistic density dependence.

Importance of Initial Conditions

The results illustrated thus far represent an averaging across quite different initial conditions. Initial conditions on population size and prairie pond numbers often influenced convergence times, but sometimes differed depending on which a priori model was used to generate time series. One obvious trend was that convergence rates were faster when simulations were started with a high initial number of ponds (6 million). Predictions of recruitment differed the most with high levels of

Table 1. Convergence times for predictor models when that predictor model was used to generate time series of midcontinent mallard abundance. A priori models represent combinations of compensatory (S_C) or additive (S_A) mortality and strongly (R_S) or weakly (R_W) density-dependent recruitment. Convergence is defined as the first time the model weight for the correct model surpasses 0.95.

A priori model	Predictor uncertainty level	Convergence time ^a	SE ^a	Proportion of time model weight <0.95 after convergence ^a	SE ^a	Proportion of simulations not converging
$S_C R_S$	1	7.626	8.020	0.253	0.300	0.113
$S_A R_S$	1	5.223	4.154	0.033	0.114	0.005
$S_C R_W$	1	3.053	1.880	0.002	0.017	0.000
$S_C R_W$	1	6.408	4.236	0.012	0.039	0.000
$S_C R_S$	2	20.739	12.176	0.099	0.167	0.527
$S_A R_S$	2	18.393	7.841	0.033	0.074	0.007
$S_C R_W$	2	8.243	2.516	0.002	0.008	0.000
$S_A R_W$	2	18.888	5.878	0.012	0.042	0.002
$S_C R_S$	3	33.250	9.322	0.062	0.107	0.960
$S_A R_S$	3	40.766	7.174	0.110	0.210	0.593
$S_C R_W$	3	14.063	2.907	0.002	0.008	0.000
$S_A R_W$	3	38.240	6.749	0.025	0.101	0.075

^a Conditional on simulation converging within 50 time steps.

ponds. Also, high levels of recruitment allowed the population to grow quickly. For models $S_A R_S$, $S_A R_W$, and $S_C R_W$, convergence was faster when simulations were started with a high population size (10 or 13 million). Complete simulation output over all models and initial conditions are available from the first author.

Level of Uncertainty

The level of system uncertainty influenced convergence rates decisively. Learning rates were slower for higher levels of uncertainty, with less rapid change of model weights following bad predictions. The estimated probability ($p_i(X1_t, X1_{t+1})$) associated with a bad prediction was impossible to estimate precisely when it occurred in extreme tails of empirical predictor distributions, regardless of bandwidth selection. Adding an increased number of components

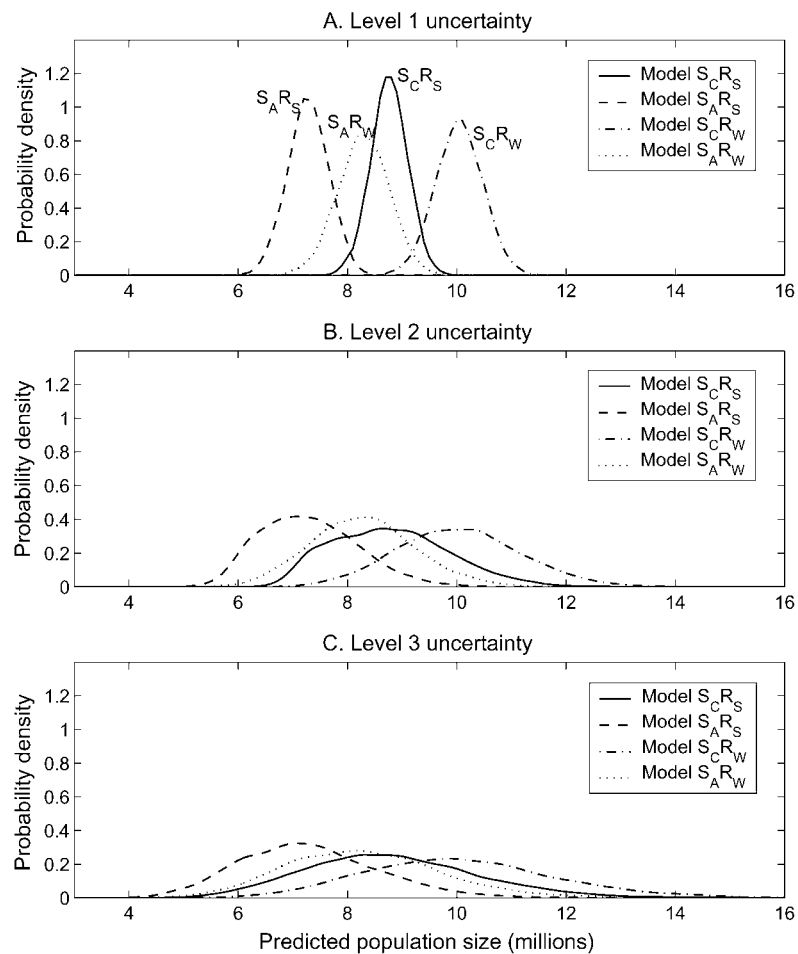


Fig. 6. Kernel density estimates of predicted population size distributions of midcontinent mallards for 1 time step under liberal harvest regulations, an initial population size estimate of 10 million mallards, and an initial spring ponds estimate of 2 million. A priori models represent combinations of compensatory (S_C) or additive (S_A) mortality and strongly (R_S) or weakly (R_W) density-dependent recruitment.

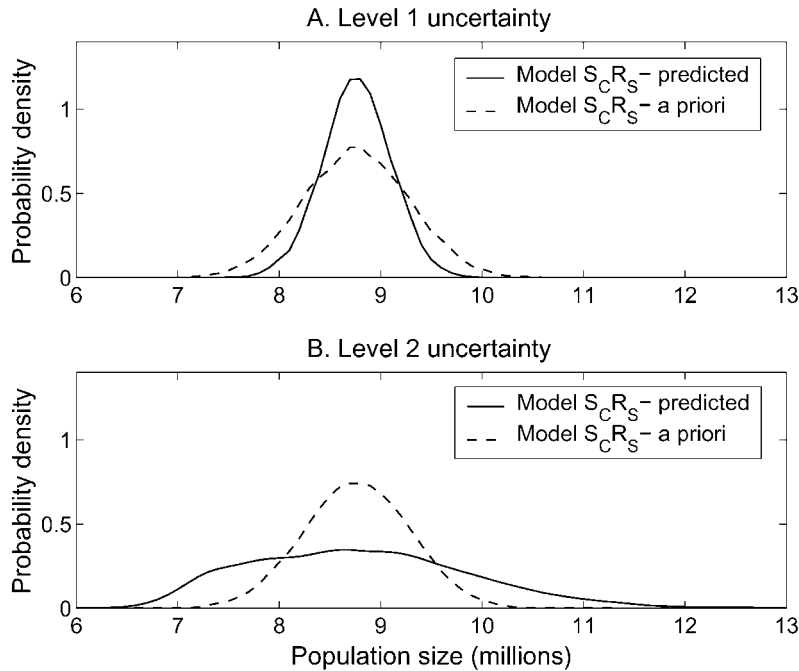


Fig. 7. Possible true population sizes of midcontinent mallards simulated by an a priori model contrasted with projections from predictor models. In (A), the predictor model incorporating Level 1 uncertainty does not include enough variation; while in (B), the predictor model incorporating Level 2 uncertainty includes more variation than the a priori model. Model $S_C R_S$ designates compensatory mortality and strong density dependence in recruitment.

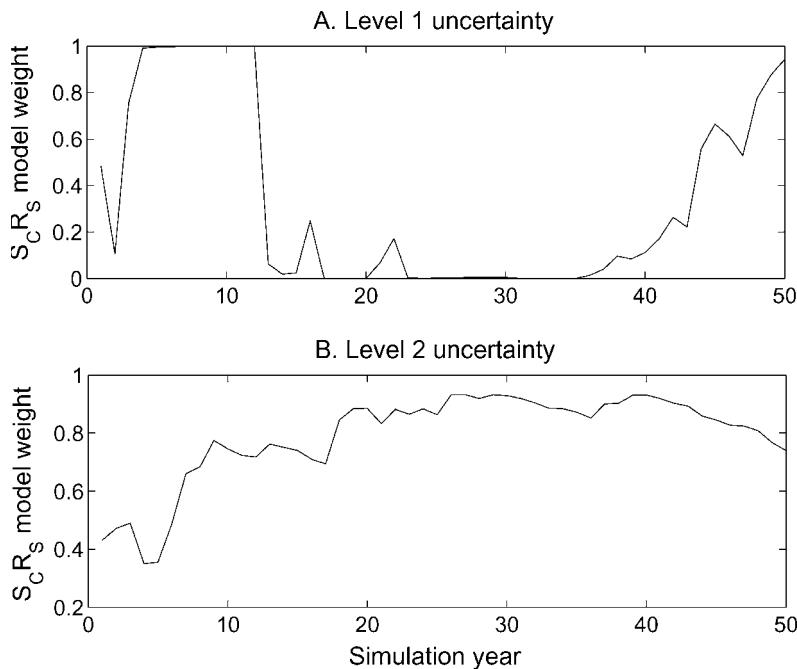


Fig. 8. Sample paths of predictor model weight for 1 iteration when model is used to generate time series of midcontinent mallards abundance. Model $S_C R_S$ designates compensatory mortality and strong density dependence in recruitment.

of uncertainty to predictions led to increasingly overlapping predictor distributions for all 4 models (Fig. 6).

DISCUSSION

Perhaps not surprisingly, when the a priori model for generating population sizes was a variant of 1 of the predictor models, convergence occurred fastest when observed population sizes occurred outside of the range predicted by other models in the model set. In this case, more extreme models such as $S_A R_S$ and $S_C R_W$ converged the fastest, while intermediate models such as $S_A R_W$ and $S_C R_S$ were slower to converge. In particular, a heavier-tailed distribution and similar predictions over the range of observed data allowed model $S_A R_W$ to usurp relative credibility from model $S_C R_S$ (Fig. 6). The fact that this phenomenon occurred when both too little and too much uncertainty was assumed about the system indicates that model selection in adaptive management may not be a trivial matter, particularly when alternative models predict similar population sizes under different mechanisms (e.g., combinations of density-dependent recruitment and survival). In such cases, employment of active adaptive management (Walters and Hilborn 1978, Walters and Holling 1990, Williams 1996) or experimental manage-

Table 2. Average predictor model weights for landmark simulation times of 3, 8, 15, 30, and 50 years when the partial compensatory survival (S_P) model is used to generate system states of midcontinent mallard abundance. In addition to partial compensation, a priori models could include strongly (R_S) or weakly (R_W) density-dependent recruitment.

A priori model	Predictor		Model $S_C R_S$		Model $S_A R_S$		Model $S_C R_W$		Model $S_A R_W$	
	uncertainty level	Simulation timestep	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
$S_P R_S$	1	3	0.266	0.332	0.406	0.371	0.065	0.149	0.263	0.288
$S_P R_S$	1	8	0.150	0.303	0.318	0.404	0.000	0.005	0.532	0.410
$S_P R_S$	1	15	0.058	0.201	0.204	0.370	0.000	0.000	0.739	0.394
$S_P R_S$	1	30	0.006	0.068	0.095	0.281	0.000	0.000	0.899	0.287
$S_P R_S$	1	50	0.000	0.000	0.060	0.230	0.000	0.000	0.940	0.230
$S_P R_W$	1	3	0.146	0.263	0.104	0.200	0.364	0.382	0.385	0.362
$S_P R_W$	1	8	0.088	0.240	0.001	0.020	0.412	0.450	0.499	0.445
$S_P R_W$	1	15	0.014	0.107	0.000	0.000	0.402	0.467	0.585	0.467
$S_P R_W$	1	30	0.000	0.000	0.000	0.000	0.351	0.465	0.649	0.465
$S_P R_W$	1	50	0.000	0.000	0.000	0.000	0.319	0.455	0.681	0.455
$S_P R_S$	2	3	0.294	0.140	0.316	0.163	0.117	0.120	0.273	0.129
$S_P R_S$	2	8	0.269	0.197	0.301	0.199	0.011	0.025	0.418	0.178
$S_P R_S$	2	15	0.202	0.203	0.230	0.225	0.000	0.001	0.568	0.228
$S_P R_S$	2	30	0.077	0.130	0.117	0.184	0.000	0.000	0.807	0.208
$S_P R_S$	2	50	0.019	0.064	0.046	0.121	0.000	0.000	0.935	0.134
$S_P R_W$	2	3	0.213	0.123	0.125	0.149	0.313	0.151	0.349	0.135
$S_P R_W$	2	8	0.175	0.166	0.010	0.034	0.377	0.229	0.437	0.217
$S_P R_W$	2	15	0.075	0.129	0.000	0.000	0.411	0.276	0.514	0.264
$S_P R_W$	2	30	0.009	0.042	0.000	0.000	0.391	0.316	0.600	0.313
$S_P R_W$	2	50	0.000	0.003	0.000	0.000	0.342	0.331	0.658	0.331

ment (Walters and Green 1997) appears necessary to reduce confounding between the models. In the case of mallards, new software (Lubow 1997) has enabled practitioners to use active adaptive optimization (Williams 1996, Williams et al. 2002) to determine optimal harvest strategies. The

active adaptive optimization procedure explicitly anticipates the gain in information that is expected to result from employment of each regulatory alternative and incorporates the utility of this knowledge into making better management decisions. Thus, if the value of discriminating between

Table 3. Average predictor model weights for landmark simulation times of 3, 8, 15, 30, and 50 years when the logistic model for density-dependent winter survival (S_L) is used to generate system states of midcontinent mallard abundance. A priori models could include strongly (R_S) or weakly (R_W) density-dependent recruitment.

A priori model	Predictor		Model $S_C R_S$		Model $S_A R_S$		Model $S_C R_W$		Model $S_A R_W$	
	uncertainty level	Simulation timestep	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
$S_L R_S$	1	3	0.153	0.258	0.584	0.388	0.062	0.140	0.201	0.282
$S_L R_S$	1	8	0.038	0.158	0.611	0.419	0.000	0.001	0.351	0.397
$S_L R_S$	1	15	0.004	0.055	0.537	0.451	0.000	0.000	0.459	0.450
$S_L R_S$	1	30	0.000	0.000	0.437	0.458	0.000	0.000	0.563	0.458
$S_L R_W$	1	50	0.000	0.000	0.380	0.461	0.000	0.000	0.620	0.461
$S_L R_W$	1	3	0.229	0.303	0.268	0.340	0.078	0.162	0.425	0.360
$S_L R_W$	1	8	0.168	0.312	0.047	0.182	0.002	0.020	0.784	0.341
$S_L R_W$	1	15	0.062	0.204	0.007	0.075	0.000	0.000	0.932	0.216
$S_L R_W$	1	30	0.016	0.117	0.002	0.041	0.000	0.000	0.982	0.123
$S_L R_W$	1	50	0.000	0.010	0.002	0.041	0.000	0.000	0.998	0.042
$S_L R_S$	2	3	0.224	0.160	0.441	0.224	0.092	0.116	0.243	0.138
$S_L R_S$	2	8	0.129	0.180	0.524	0.233	0.005	0.013	0.342	0.189
$S_L R_S$	2	15	0.043	0.116	0.540	0.258	0.000	0.000	0.417	0.239
$S_L R_S$	2	30	0.002	0.021	0.488	0.295	0.000	0.000	0.510	0.293
$S_L R_S$	2	50	0.000	0.001	0.422	0.326	0.000	0.000	0.578	0.326
$S_L R_W$	2	3	0.261	0.138	0.272	0.178	0.133	0.125	0.333	0.144
$S_L R_W$	2	8	0.257	0.190	0.131	0.151	0.027	0.051	0.585	0.203
$S_L R_W$	2	15	0.152	0.179	0.038	0.092	0.001	0.003	0.810	0.187
$S_L R_W$	2	30	0.033	0.086	0.001	0.015	0.000	0.000	0.966	0.087
$S_L R_W$	2	50	0.002	0.010	0.000	0.000	0.000	0.000	0.998	0.010

models is high (in terms of the objective function), active optimization might help resolve problems with confounding models by probing into regions of the state and decision space that are not usually accessible (e.g., dictating a liberal or moderate regulation in a year of small population size). In this exercise, faster convergence occurred when population sizes were high. Ostensibly, this was because the difference between compensatory and additive model predictions was the greatest when the population was harvested according to a liberal harvest package. A moderate or restrictive harvest package likely would be implemented with smaller population sizes.

The 4 predictor models we used embody extreme hypotheses about processes underlying population dynamics. However, the functional form that best approximates these processes may be different than specified in predictor models (Runge and Johnson 2002). For the partial compensation and logistic winter survival cases we investigated, model selection largely favored predictor model $S_A R_W$, which had heavier tails and predicted population sizes that were intermediate among other predictor models (Fig. 6). Under the completely compensatory phenomenological model, no mortality is modeled for harvest rates ≤ 0.15 because of the assumption that increased survival of other individuals offsets such losses. The changes in winter survival postulated in the logistic model for individuals surviving the hunting season (Fig. 3) did not appear to be large enough to promote convergence to a compensatory model. However, the logistic model we employed could have been parameterized differently and also could have incorporated a component for summer survival. Analyses of current large-scale mallard data have not produced sufficient evidence to support hypotheses of density-dependent summer survival (W. L. Kendall, USGS, and D. I. MacKenzie, Proteus Research and Consulting, unpublished data). However, some confirmatory evidence has been found for such an effect in the past when twice-a-year banding programs permitted direct estimation of summer survival (e.g., Nichols et al. 1982, Johnson et al. 1992). In general, the power to test for seasonal density dependence is low because yearly parameter estimates are imprecise and density can affect harvest rates as well as nonhunting survival (Smith et al. 1992). Thus, different parameterizations of the logistic model may have yielded different results.

Learning rates slow dramatically as more uncertainty is assumed about the system, causing

model-specific probability distributions for predicted population sizes to increasingly overlap. Identifying the candidate predictor model most likely to have given rise to the observed data takes much longer in these scenarios. That is, if nature is reasonably approximated by 1 of the predictor models, assuming more uncertainty about the system will make identification of the correct model take longer. On the other hand, using a smaller number of variance components than should be included (e.g., assuming more knowledge about the system than is realistic) can lead to rapid change in model weights following particularly bad predictions. In this case, learning appears to consist of identifying the model or models that have best explained population changes over a short time period. Mathematical problems also can occur with estimating probabilities in the extreme tails of predictor distributions (e.g., 4 or 5 SD from the mean) when insufficient sampling and process errors are included in model predictions.

The fact that models $S_A R_W$ and $S_A R_S$ had acquired virtually all of the model weight by 2001 following institution of mallard AHM in 1995 (U.S. Fish and Wildlife Service 2001) is consistent with analysis of the most recent banding data (Smith and Reynolds 1992; J. E. Hines, USGS, unpublished data). However, previous analyses had yielded contrary evidence for the mortality model most appropriate for mallards (e.g., Burnham and Anderson 1984, Nichols et al. 1984). Results from our simulations may illuminate several possible causes for convergence to additive mortality models. First, because no individual model predicted well over all years, the true model for population dynamics may have a greater number of variance components than any of the predictor models. This makes intuitive sense because quantities such as crippling loss and nonhunting season survival should ultimately be modeled as random variables instead of fixed parameters. Second, the real-world biological factors determining population sizes may be best approximated by a model that is not in the model set, perhaps with a combination of hypotheses, different functional forms of hypotheses, or important mechanisms that have not yet been elucidated. In light of simulation results, a reasonable possibility is that model selection in this case would favor model $S_A R_W$. A third possibility not considered here, but potentially important, is that the model set includes 1 model whose structure reasonably represents truth but whose parameters are estimated with bias. This issue was raised and adjusted for in 2002 (U.S. Fish and

Wildlife Service 2002) and produced model weights that were not as extreme.

MANAGEMENT IMPLICATIONS

Results from these simulations indicate that errors in model selection could have occurred in mallard AHM as practiced from 1995 to 2001. Original predictor model sets likely did not include enough uncertainty components. The evolution of model weights among AHM predictor models may have been a real result of learning but could also be explained by stochastic events occurring over a wider scale than anticipated by any 1 predictor model. For instance, random variation in natural mortality could have perturbed population sizes outside the range of a model's predictions, even if the recruitment and harvest mortality hypotheses of that predictor model reasonably represented reality. These concerns, along with others beyond the scope of this study, have been addressed within the mallard AHM community, most notably by reformulation of the predictor model set in 2002.

Wildlife managers, along with any scientists enlisted in the process, should give considerable care to translating ecological hypotheses (e.g., recruitment is density dependent) into predictive models (e.g., what should be the actual parameter values under each model). These considerations include uncertainty associated with each parameter (i.e., sampling variability of those estimated from real data) and how those parameters vary over time or space (i.e., process variation). Our results illustrate some of these concerns, indicating potential problems with model selection in certain adaptive management scenarios. In addition to including all sources of uncertainty, predictor distributions should all have a similar variance structure so that predictor models with long-tailed distributions do not gain unfair advantage in the model-selection process. While difficult to parameterize in practice, wildlife and fisheries managers should consider mechanistic functions for density-dependent survival as alternatives to phenomenological models to better represent uncertainty about the appropriate functional form for population dynamics. Practitioners of adaptive management also should conduct simulation experiments to determine possible complications and alternative explanations for changes in model weight. Additional problems with model selection may be eliminated by experimental perturbations of the system (Walters and Hilborn 1978, Walters and Holling 1990, Carpenter et al. 1994), ideally within an active

adaptive optimization (Williams 1996, Williams et al. 2002) framework.

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Appendix A. Methods used to separate process and sampling error in recruitment functions of a priori models.

Skalski and Robson (1992) showed that

$$E[S^2] = \sigma^2 + \frac{1}{n} \sum_{j=1}^n E[\text{Var}(\hat{R}_j | F)] - \frac{2}{n(n-1)} \times \sum_{j < k} \{ \text{Cov}(R_j, R_k) + \text{Cov}(\hat{R}_j, \hat{R}_k | F) \},$$

where F denotes all of the information in nature's realization of the R_j (Link and Nichols 1994). If unbiased estimates of sampling variance and covariance are available, this equation can be rearranged to obtain an estimate of true temporal variability given by

$$\hat{\tau}^2 = S^2 - \frac{1}{n} \sum_{j=1}^n \hat{E}[\text{Var}(\hat{R}_j | F)] + \frac{2}{n(n-1)} \times \sum_{j < k} \hat{E}[\text{Cov}(\hat{R}_j, \hat{R}_k | F)],$$

(Link and Nichols 1994, Gould and Nichols 1998). Making an additional assumption that the sampling covariance is zero, the process variation can be estimated as

$$\hat{\tau}^2 = S^2 - \frac{1}{n} \sum_{j=1}^n \hat{E}[\text{Var}(\hat{R}_j | F)]. \quad (1)$$

Recruitment estimates from 1970–1993 were used to compute a mean squared error for each recruitment model, which can be substituted directly into Eq. (1). However, estimating the remaining piece,

$$\sum_{j=1}^n \hat{E}[\text{Var}(\hat{R}_j | F)],$$

requires some creativity, as direct estimates of yearly sampling variances for fall age ratios are not available. Instead, these fall age ratios are determined by dividing raw age ratios (\mathfrak{R}_j) by partial vulnerabilities to harvest (V_j), both of which are determined by yearly parts collection surveys. To compound problems, partial vulnerabilities and associated sampling variances have traditionally been estimated with respect to adult males. To get an approximate estimate for sampling variances of partial vulnerabilities for young females to adult females, we calculated the absolute variance of partial vulnerability to harvest for years 1961–1993. That is, we made the approximation

$$\hat{E}[\text{Var}(\hat{V} | F)] \approx \text{Var}(\hat{V}).$$

We applied this approximation of sampling variance to all years, which introduced autocorrelation into the variance structure, but we ignored this problem in the interest of obtaining a somewhat meaningful estimate of process error. Fortunately, estimates of sampling variance were available for raw fall age ratios of adult females to young females over the years 1961–1993. We used a first-order Taylor series approximation for the variance of a ratio (Casella and Berger 1990) to compute

$$\hat{E}[\text{Var}(\hat{R}_j | F)] \approx \hat{E}\left[\text{Var}\left(\frac{\mathfrak{R}_j}{V_j} | F\right)\right].$$

Process variance could then be estimated as 0.0059 and 0.0082 for the weakly density-dependent recruitment model and strongly density-dependent model, respectively.